

VII. *On Diaposematism, with reference to some limitations of the Müllerian Hypothesis of Mimicry.* By GUY A. K. MARSHALL, F.Z.S.

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ONE of the most striking features in connection with the philosophical study of the phenomena of Mimicry among butterflies in recent years has been the marked tendency to lay an ever increasing emphasis upon the importance of the selective factors suggested by Fritz Müller and to minimise the influence of what is known as Batesian Mimicry. It has even been suggested that every known case of mimicry among butterflies can be more satisfactorily interpreted as being due to the operation of Müller's principle. The essential difference between these two theories of mimicry lies in the fact that one explains how an edible (or less unpalatable) species will derive advantage through assuming a superficial likeness to another which possesses nauseous (or more unpalatable) qualities (Batesian mimicry); whereas the other shows how one nauseous species will benefit by mimicking another having the same qualities (Müllerian mimicry). Now although there can be little doubt that a good many cases of mimicry originally adduced in support of Bates' theory must now be explained on Müllerian lines; yet the universal application of this latter principle to butterflies, involving, as it does, the assumption of unpalatability in every mimic, seems open to some serious objections which may be considered later.

Perhaps the principal stimulus to the recent extension of Müller's interpretation of mimetic resemblances has been furnished by an hypothesis which has been developed by Dr. F. A. Dixey. It was in his important and able memoir on the Phylogeny of the Pierinæ (Trans. Ent. Soc., 1894, pp. 249-334) that Dr. Dixey first outlined his conception of Diaposematism, or Reciprocal Mimicry, as it was then called. This conception consists practically of a widening or complication of the principle put forward by Müller to explain the inter-resemblances between distasteful butterflies belonging to different genera. For

although Müller evidently conceived, and briefly mentioned, the possibility of a mutual approach between two such species (Proc. Ent. Soc. 1879, p. xxviii), yet his theory was generally interpreted as involving only a one-sided approach from one species to another. On the other hand the hypothesis of Diaposematism specially emphasises the probability of a mutual simultaneous approach. To use the author's own words: "There seems to be no reason why, especially if there is no conspicuous inequality of numbers, there should not be a kind of 'give and take' arrangement between mimicker and mimicked, the latter advancing some way to meet the former for their mutual benefit. In other words, when two species, A and B, form an association of this kind, it need not be supposed that the form of A remains fixed, while B assimilates itself to it, or *vice versa*; but the association may really be formed by both A and B converging to a point between them, or, in short, mimicking each other. The acceleration of the process, which in many cases would result, must of itself be an advantage." (Trans. Ent. Soc. 1894, p. 297.) And again: "In the latter case (Müllerian Mimicry) the mimetic attraction is unlimited and mutual, acting reciprocally in both directions, and influencing each member of the group." (Trans. Ent. Soc. 1897, p. 325.) This line of argument was also advocated in the Transactions for 1896 (p. 72), and since that time various specific cases have been published by Dr. Dixey, Professor Poulton and Mr. S. A. Neave, which are considered to furnish convincing proof of the validity of the hypothesis of reciprocal mimicry. Indeed, it has been held that these proofs are so cogent that Diaposematism should no longer be regarded as a mere hypothesis, but that it is now entitled to rank as an established law (Proc. Ent. Soc. 1906, p. lxxi).

But before looking into the details of these cases it may be well to examine the whole conception from a more general standpoint. It has already been remarked that reciprocal mimicry is merely a complication of Müller's theory, and it is therefore important to have a very clear idea of the essential nature of that theory, of the factors which make for a Müllerian Association, and of the conditions which are most favourable to its development. The real starting-point for the Müllerian hypothesis lies in the proposition (sufficiently well established by now)

that young insectivorous animals are not born with an instinctive knowledge of what insects are good to eat and what are not. The slow flaunting flight and conspicuous coloration of a *Danaida* or a *Heliconius* can have no special significance for a young bird when it first starts out in life to forage for itself. The knowledge that these butterflies possess a pronouncedly unpleasant flavour can only be acquired as the result of direct experiment, and probably several butterflies would be destroyed by such a bird before it succeeded in permanently associating the conception of unpleasantness with any particular colour-pattern. Thus each species with an independent type of warning coloration would have to lose a certain percentage of its individuals before its true significance could become a matter of common knowledge among all the young and inexperienced insect-eaters in any particular neighbourhood. From this Müller argued that if two such species, having different colour-patterns and inhabiting the same area, were to develop the necessary variations leading up to a mimetic association, such a combination would be of considerable utility in relation to the experimental tasting of young birds; for then both species together would only have to contribute the same number of victims which each of them would have to furnish if their colours were different.

Given the initial variation, such a mimetic resemblance can only be built up through the operation of some eliminative or selective factors which shall result in an advantage to the variation as compared with the typical form from which it is derived; thus leading up to the gradual replacement of the latter by the former. And it may be noted that, with the exception of resemblances in which mere affinity has obviously played a great part, the closer the mimicry, the greater must have been the persecution of the mimic (whether Batesian or Müllerian) and the higher the percentage of its elimination. In the case of Müllerian mimicry, as we have seen, the selective agent is provided by the destruction due to the experimental tasting of unpalatable insects by inexperienced insectivorous animals. This may be briefly denoted as the "Müllerian factor."

There are certain points in connection with the operation of this factor which it is well to bear in mind. In the first place, the differences in the relative intelligence of

the butterflies' enemies will affect the results due to their attacks. Those which exhibit a high degree of intelligence will obviously profit more quickly by their experience; in other words, they will acquire the necessary mental association between colour and inedibility by the destruction of comparatively few butterflies. They will therefore operate much less efficiently as producers of Müllerian mimicry than will those enemies which have a comparatively low degree of intelligence and which therefore require to make many experiments before arriving at the same result. But if there be enemies still lower in the scale and incapable of forming such a mental association at all, then the destruction of butterflies which they would cause would have no effect whatever from a purely mimetic standpoint; no more than if the insects had been killed by a torrential thunderstorm. Similarly if we suppose that a certain species of bird has specially adapted itself to feed on a genus of insects usually avoided by other insectivorous animals, the attacks of that bird will have no effect in the direction of Müllerian mimicry on that particular genus. In other words, the mental attitude of the enemy towards its prey has an important bearing upon the results which its attacks will produce. Finally, the accumulation of experience does not render an animal more effective as a Müllerian factor, but precisely the reverse; for as it becomes more skilled in recognising nauseous species, so will it gradually cease its experimental destruction, upon which this kind of mimicry so essentially depends.

If we turn for a moment to consider whether these arguments are equally applicable in the case of Batesian mimicry, we find, on the contrary, a totally different state of affairs. So far from experience and intelligence being adverse qualities, it is evident that the greater the accumulation of experience and the higher the degree of intelligence possessed by the insectivorous animal, the greater will be its efficiency as a producer of Batesian mimicry. For it will thus be the better enabled to discriminate between the edible mimic and its inedible model, with the result that there will be a more effective selection and a keener elimination of those variations of the mimic which do not come up to a high standard of resemblance. A consideration of this difference in the operation of these two mimetic forces would appear to

justify the expectation that the elimination due to the Batesian factor would be competent to produce a higher degree of inter-resemblance than would the factor adduced by Fritz Müller.

Another point worth noting is the difference in the periods of incidence of these two processes of selection. The Müllerian factor is, as we have seen, supplied entirely by young and inexperienced birds, etc.; it will therefore have its greatest effect during the summer months when such young animals would be most numerous. As the season advances, however, these animals would be increasing in wisdom and experience, and consequently by the autumn or early winter we may reasonably suppose that their efficiency as producers of Müllerian associations will have very notably diminished. Now from this time onwards until the early months of the next summer there will be no further appearance of young broods of insectivorous animals; and it seems clear that for a considerable portion of the year the forces which make for Müllerianism will be at a very low ebb, if not altogether absent. On the other hand, there seem to be no grounds for assuming the existence of any such period of marked diminution in the factors which make for Batesian mimicry; for in most tropical countries butterflies (which are here alone being considered) are fairly plentiful throughout even the winter months, while there is a much greater reduction in the insects of most other orders (*cf.* *Trans. Ent. Soc.* 1902, p. 432). Thus, although a large number of insectivorous migrants will have departed at that season, the scarcity of other insects, in conjunction with the comparative conspicuousness of butterflies, will doubtless lead to a maintenance, or even an increase, of the percentage of destruction by the remaining resident birds. The incidence of Batesian elimination, therefore, will be comparatively continuous and persistent.

Having thus briefly examined some aspects of Müller's selective factor, we may now endeavour to ascertain the conditions which will render it most effective in fostering mimetic associations. The position of affairs will be best appreciated by taking some hypothetical case. Let us assume therefore that within any given area there exist two species of butterflies, A and B, possessing nauseous qualities in about the same degree, but having different warning colour-patterns; and further that within the

same area the education of young birds, lizards, etc., necessitates the destruction of approximately 1000 individuals in each group of distinctive patterns. Again, let us suppose that A is a common species and is represented by 100,000 individuals in that locality, while B is more scarce and has only 5000. Now, *ex hypothesi*, the Müllerian factor will exact an equal toll from the two species, and its selective importance must therefore depend upon their relative numbers. In the present instance the plentiful A will lose only 1 per cent. of its individuals from this cause, while the scarcer B will lose no less than 20 per cent. It is therefore reasonable to suppose that if certain individuals of B chanced to develop a variation in the direction of A, that variation would have, in relation to the Müllerian factor, a definite advantage over its own typical form, because it would tend to share, at least to a small extent, in the relative advantage enjoyed by A; and the continuance of the elimination would gradually tend to enhance the variety and to diminish, and finally exterminate, the type. This would be a case of simple Müllerian approach from B to A. But if the mimicry is to be reciprocal it must be shown that A is capable of approaching B by a precisely similar process. In order to simplify the argument let us make the supposition that 10,000 specimens of A simultaneously present a sudden marked variation in the direction of B, to such an extent that young birds would be liable to rank them with B rather than with A; what will be the effect of the Müllerian factor on this remarkable variety? The point again to be considered is the relative incidence of the destruction. There will now be 90,000 examples of the A pattern, and 15,000 of the B pattern. If 1000 individuals of each are again destroyed by experimental tasting, a simple calculation shows that the percentage of loss due to this factor will be six times greater in the variety of A than in the typical form of A. In fact the result is exactly the opposite of what took place in the case of the variety from B towards A. Whereas there we found that the variety had an appreciable advantage over its own type form, here it is seen to be at a distinct disadvantage. It is obviously impossible for the Müllerian factor to build up a mimetic resemblance on such a foundation; if it have effect at all, that effect must be to gradually eliminate the variety and to establish

the type form. In these particular circumstances it is clear that the simultaneous and mutual mimicry, postulated by the hypothesis of Diaposematism, is entirely out of the question. The Müllerian factor is capable of converting B into a mimic of A, but it cannot cause A to mimic B.

This simple example illustrates several interesting points. In the first place, it shows that the whole idea of Müllerian mimicry practically resolves itself into a numerical computation of the relative percentages of loss. The only kind of variation which can have any significance will be one that shall be trending from a form having a higher percentage of loss towards one having a lower percentage; so that a difference in these percentages is an essential condition for the production of Müllerian mimicry. But Müller's hypothesis postulates that the absolute destruction is practically constant for each group of different colours, and therefore the necessary conditions can arise only where there is a noticeable difference in the initial numbers of the two species involved. Further, the greater the discrepancy between these two numbers, the greater will be the advantage derived by any variation from the rarer species in the direction of the more numerous, and consequently the more powerful and rapid will be the operation of the Müllerian factor in producing a mimetic approach. This therefore constitutes the most highly favourable condition for the evolution of Müllerian mimicry. Conversely, as the numbers approach one another, so will the value and importance of the initial variation from the numerically smaller species towards the larger become less and less; so too will steadily diminish the effectiveness of the Müllerian factor as a producer of mimicry. Finally, when we arrive at a case where the two species are equal in numbers, there will then be a condition of equilibrium, and the Müllerian principle will practically cease to operate altogether.

So far as concerns the variations which may arise from the numerically larger species towards the smaller, these will be the more rapidly exterminated, the greater the discrepancy in the numbers of the two species. As this difference diminishes, the disadvantage of such a variety, as compared with its typical form, will also diminish; but in no case can its development be fostered and increased through the medium of the Müllerian factor, because it still remains a variation in a disadvantageous direction.

Further, as the numbers approach each other, any variation from the larger towards the smaller tends to produce equality, a condition which effectively prevents the Müllerian selection from producing any mimetic results. We see then that a Müllerian approach will only take place in one direction, namely, from a rarer species towards a more abundant one, and no species can in this way approach another which has fewer individuals (and therefore a higher percentage of loss) than itself.

If this conception of the conditions which make for Müllerian mimicry be accepted as sound, it would appear that the hypothesis of Diaposematism is placed on the horns of a veritable dilemma. For this hypothesis differs in no real essential from Müller's principle, of which it appears to be merely an extension; and yet we find that the very conditions which are most highly favourable for a simple Müllerian approach are at the same time absolutely fatal to anything in the way of reciprocal mimicry. On the other hand, this latter conception only begins to appear feasible at the other end of the series, namely, where the numbers of the two species approximate equality. But we have seen that this is a condition which renders any occurrence of Müllerian mimicry in the highest degree improbable; and there can be no Diaposematism where there is no Müllerian mimicry. In my opinion, the above considerations render it difficult to accept the essential idea of reciprocal mimicry even as a mere working hypothesis.

Now it may be urged that the statement as to the practical impossibility of Müllerian mimicry when the numbers of the two species are equal cannot be maintained, and that its unsoundness can be demonstrated by some such illustration as the following. Supposing that A and B are each represented by 20,000 individuals and that they lose 1000 apiece from experimental tasting when their colours are different; then if they enter into a mimetic association they will only lose 1000 out of 40,000; in other words, their losses from this cause will be reduced by one-half. Here is a clear and decided advantage, and therefore it may be claimed that the Müllerian factor must have scope to produce such a mimetic approach.

But before hastening to accept this conclusion it is well

to point out that unless due care be exercised in the use of this kind of argument from advantage, it is liable to lead to erroneous conceptions. In order to show this more clearly let us apply the same line of argument to a slightly different case. If we suppose that there are 20,000 examples of A and only 10,000 of B, each losing 1000; then when A stands alone it will lose 5 per cent. of its numbers. But if A develops a mimetic tendency in the direction of B, and finally becomes a mimic of that species, then its loss from experiments will be reduced to only $3\frac{1}{2}$ per cent. Here again there is a clear advantage as compared with its previous condition, therefore it will be claimed that the Müllerian factor must be capable of converting A into a mimic of B.

Now we have already seen that where the numbers of A are considerably in excess of those of B, as in this case, any initial variation (in the Darwinian sense) from A towards B will be going from a lower percentage of loss in the direction of a higher percentage, and that therefore that variation will be at a disadvantage as compared with its own type form, in relation to the factor which is causing the loss. In such circumstances therefore the Müllerian factor cannot convert A into a mimic of B.

Here then these two lines of argument, based on the same data, have led to diametrically opposite results. The reason for this divergence is not far to seek. It will be observed that the contention in favour of a Müllerian approach from A to B is based entirely on a consideration of the advantage which would accrue *when the mimicry had become an accomplished fact*, while the intermediate stages are in no way taken into account. But the whole Darwinian idea of the evolution of such a case of mimicry involves the assumption that it has been built up by a gradual process of selection from comparatively small individual variations. Therefore the essential point to be considered must be the question of relative advantage as between the *initial* variation and its typical form; and the assumed ultimate advantage has no real significance unless it can be shown that the initial variation has some definite advantage over the type in relation to the selective factor which is considered to cause the mimetic approach. Where this point is overlooked, an argument based merely on a supposed eventual gain may, in some cases, be entirely misleading.

On reverting to the case where the two species have equal numbers and applying the above test, we find that the contention in favour of a Müllerian approach cannot reasonably be maintained. If A and B are equal, then their position in regard to the Müllerian factor is absolutely identical, so that neither has an iota of advantage over the other and the essential condition for the origin of Müllerian mimicry is lacking. In these circumstances it is evident that any small variation from one towards the other will not practically affect the numerical relationship of the two species and will therefore have no mimetic value.

The comparative numbers of individuals in Müllerian Associations.

Unfortunately we have very little knowledge as to the approximate individual numbers of the species forming any Müllerian association; but in November 1903, Professor Poulton exhibited to this Society (Proc. Ent. Soc. 1903, p. liv) a series of 323 butterflies captured on a single day by Mr. C. B. Roberts in British Guiana, with a view to giving an idea of the relative numbers of the species in that spot. Out of the total no less than 295 specimens, comprising 9 species, fell into the mimetic association which centres round the common *Melinæa mneme*, all of them belonging to undoubtedly distasteful genera. *M. mneme* itself vastly outnumbered the other species, being represented by 253 individuals, while the remaining 8 species were represented by the following numbers: 8, 9, 10, 9, 1, 3, 1, 1. There seem good grounds for supposing that these figures do give a fair rough idea as to the relative occurrence of these species in that locality, and the very striking discrepancy in the numbers of the mimics as compared with their dominant model is precisely what we should expect to find on the conception of Müllerian mimicry here advocated. Such conditions would be specially favourable to the production of a large mimetic association, and it seems highly probable that in actual practice Müllerian mimicry will only have arisen where the discrepancy in numbers has been fairly considerable; although the possibility of its occurrence where the difference is comparatively small can, of course, be theoretically upheld.

Alternating Resemblance.

Although there appear to be serious difficulties in the way of accepting any idea of mutual simultaneous mimicry between two unpalatable species, yet it is not impossible that a certain interchange of characters might still take place between them. For example, at first A might be more numerous than B and a simple Müllerian approach might take place from B towards A. While this was in progress conditions might arise which would cause a reversal in the relative numbers of the two species, so that B would become the dominant partner. Then any further mimetic approach that might take place would be from A towards B, so that the final result might show a fusion of the original colours of the two species. This kind of approach is quite different from that contemplated in the hypothesis of Reciprocal Resemblance, although producing similar results; it may therefore be distinguished under the name of Alternating Resemblance. It is not probable that this phenomenon will be of common occurrence in nature, and it is only here referred to in order to show that even if the actual existence of reciprocity can be demonstrated, that will not of itself afford proof of Diaposematism; for the facts can be consistently interpreted on the lines of a one-sided Müllerian approach.

Since the foregoing remarks were written Professor Poulton has kindly suggested to me a criticism which appears, at first sight, to lend some support to the idea of Diaposematism. As a very similar suggestion has been made to me independently by another friend, it seems advisable to show how it may be met.

It has been contended that among the enemies of the two distasteful butterflies, A and B, there will be some (which we may call X) whose first experience will be entirely of A. Having thoroughly learnt that this insect is unpalatable they will then come across B. If among the individuals of B there occurs a variation (B') which presents a roughly A-like appearance, then B' will have an advantage over B in relation to the attacks of X. Similarly other enemies (Z) will first have experience of B only, so that when they afterwards attack A, the variety A', which has varied in the direction of B, will be at an advantage as compared with A, because it will recall to

the mind of the enemy unpleasant experiences in connection with B. On these grounds it is argued that both varieties, A' and B', are advantageous, and that therefore the two species can mimetically approach one another at the same time. But a little consideration will soon show that the above argument does not deal with all the factors in the case. In the first place, the enemies are divided into only two categories (X and Z); but there must obviously be a third (Y) which will derive its knowledge through a mixed experience of A and B together, and the effect of this has been quite left out of consideration. Now it is evident that reciprocal mimicry could only take place where A and B are approximately equal. When this is the case, the law of probabilities shows that the numbers of Y will be very large, those of X and Z very small; therefore the net result of the Müllerian factor will depend upon the effect produced by Y, and this is entirely covered by the general argument set forth above, which thus remains unaffected.

There is yet another more important objection to this criticism. It is contended that X will discriminate between B and B', and Z between A and A', to the advantage of B' and A' respectively; but the relation of X to A and A', and Z to B and B' is not taken into account at all. But if A' is sufficiently different from A that Z will discriminate between them, it must be admitted that X will do so likewise. Such discrimination means that A' will be subjected to special tasting experiments by X, as apart from A. But *ex hypothesi* the numbers of A' will be very much smaller than those of A, and therefore these experiments will involve a much higher percentage of loss for A' than for A, so that the former will be at a decided *disadvantage* in relation to the attacks of X. The same applies to B' with regard to the attacks of Z. Thus A' will have an advantage over A during the attacks of Z, and a disadvantage during those of X, and the net result will depend upon the relative numbers of X and Z. But the relative numbers of X and Z are directly dependent on the relative numbers of A and B respectively; for where A is abundant the members of X will be large and *vice versa*. Therefore when A and B are equal, X and Z will be equal, and the advantage which A' derives from Z will be balanced by the disadvantage due to X; and similarly for B'. In these circumstances there will be a condition of

equilibrium so far as concerns the Müllerian factor, and no mimetic approach will take place. Again, where A is largely in excess of B, X will be large and Z small; therefore the disadvantage accruing to A' will be large, the advantage small, the net result being a considerable disadvantage; so that the effect of the Müllerian factor will be to stamp out A' and to establish A, in other words, to prevent its mimicking B. It is thus evident that so far from upsetting my general argument this criticism merely serves to confirm it when all the factors are taken into account.

We may now turn to an examination of the various cases which have been cited as furnishing conclusive evidence as to the actual occurrence of diaposematic resemblances. In looking at these as a whole an interesting fact emerges, namely, that no example has yet been brought forward as occurring between any two of the most dominant distasteful groups of the world, viz.: Danaini, Euplœini, Lycoræini, Ithomiinæ, Heliconinæ and Acraeinæ; although it is among some of these groups that Müllerian mimicry finds its highest development, and cases of reciprocity should be evident and numerous, if Diaposematism be a *vera causa*. Perhaps it is a mere coincidence that in the great majority of instances cited (5 out of 7) one of the mimetic forms belongs to a species not generally considered to be unpalatable. But it has been claimed that the establishment of a case of diaposematic resemblance is of itself good evidence of the unpalatability of both species involved. This claim is obviously justifiable only where it can be shown that it is impossible to interpret the facts on any hypothesis other than Diaposematism; and such a case has not yet come under my notice. It was in connection with this aspect of the question that I first found myself in conflict with this theory; for its application has led to the assumption that the coloration of certain South African butterflies has a warning significance, indicating the existence of distasteful qualities, whereas my own observation of the insects in the field (supported by a few experiments) has led me to an entirely opposite conclusion. These divergent results have induced me to undertake a closer examination of the foundations upon which the hypothesis of Diaposematism has been built.

I. *The Association of Pereute and Heliconius.*

This case is of special interest because, with the next one, it furnished the original basis for the theory we are considering. It was dealt with by Dr. Dixey in *Trans. Ent. Soc.* 1894, p. 296, and further discussed in the *Trans.* for 1896 (p. 72). The facts are briefly these: Certain forms of the Pierine genus *Pereute* in Tropical America exhibit an undoubted mimetic approach towards the common *Heliconius melpomene* and its allies, whose upper-side colouring is plain brown, with a broad red band across the fore-wings. Now many species of *Pereute* have on the under-side some distinct red spots at the base of the hind-wing. Somewhat similar markings also occur in the *Heliconii*, but Dr. Dixey, quite justifiably, refuses the explanation that these spots have been acquired by the *Pereute* as part of their mimetic resemblance to *Heliconius*. For he shows that not only can we find similar markings in other American Pierines which have no mimetic relationship with *Heliconius* or any of the red-spotted *Papilios*, but further they are shown to occur independently in Pierine genera in other parts of the world; notably in some species of the distasteful Eastern genus *Delias*, to which he considers *Pereute* to be nearly allied. On these grounds the spots are claimed as being Pierine in character. How then are we to explain their presence in *Heliconius*? Any argument for parallel development is rejected by Dr. Dixey, for he says: "If we assert them to be purely 'accidental,' we are met by the fact that although they are found in some species of both *Papilio* and *Heliconius* that are apparently not the subject of mimicry, yet they are most distinct and most prevalent in those species which are copied by Pierine imitators" (*l. c.* 1894, p. 296). Hence it is contended that the only satisfactory explanation is that, in this particular respect, the *Heliconii* have been influenced by, and approached, the *Pereute*, and that therefore the red spots constitute a reciprocal or diaposematic character.

Now, in order that any case of this kind may really carry conviction as a proof of diaposematism it is necessary to show that the reciprocal character which the model is claimed to have acquired from the mimic must be one that is abnormal in the genus of the model and its allies. For if the character occurs frequently and independently

in other members of the same genus its appearance in any one species might well be due to simple affinity with them and not to mimicry at all. The fact that the model and the mimic possessed *ab initio* certain superficial characters in common would of itself render a mimetic approach the more probable; yet the occurrence of these similar markings would, in no sense, be due to mimicry, and no argument for diaposematism could be founded upon them.

The first point therefore to be investigated is the occurrence of this red spotting in *Heliconius*. With the accession of the splendid Godman and Salvin collection the British Museum now possesses a very fine series of this genus. A careful examination of this material, based on Riffarth and Stichel's monograph of *Heliconius* in the "Theirreich," shows that out of the 71 species recognised by these authors no less than 35* possess basal red spots on the under-side of the hind-wings. Of the remaining 36 species about three-fourths have been drawn away in mimicry of the great *Melinæa-Mechanitis* association, and the absence of red spots may perhaps be actually due to this mimicry; for I have been unable to find that any genus of Ithomiinæ or Danainæ possesses this kind of marking. The *Heliconii* in which the red spots are present belong to various different types of coloration, several of which do not appear to be mimicked by Pierines, and in some of these the red spots are very highly developed, more so than in any non-mimetic American Pierines. Nor does there appear to be any constant connection between general mimicry and the development of the spots. For example, *Pieris locusta* ♀ roughly mimics *H. cydno-galanthus*, and the nearly allied *P. noctipennis* ♀ mimics *H. sapho-leuce* (Dixey, "Nature," Oct. 1907, p. 677); the under-side red spots of the two *Pieris* are almost identical, yet those of the *Heliconius* differ very much from them and from each other.

Turning now to *Pereute* we find that the colour of the under-side of the hind-wing may be generally described as dark brown with a variable yellow costal streak, and with, or without, two or three basal red spots. With regard to the upper-side colouring the genus may be

* It may be noted that the great majority of these species also have a red streak along the base of the costa of the fore-wing on the under-side, a character which I have failed to find in any American Pierines.

divided into three sections. In the first, comprising only the more primitive *telthusa*, the sexes are alike, being blackish, with white markings and an irroration of grey scaling; the under-side having *three* red spots. In the second the sexes are again alike, both being black, with a red bar across the fore-wing and with a very striking broad blue-grey suffusion over the bases of both wings; inferior red spots (two) present or absent. Finally, in the third section, the sexes are different, the males being blackish-brown with general grey irroration; while the females are brown, with a pink or red bar in the fore-wing, having a basal grey suffusion in the former case, and none in the latter; inferior red spots (two) present or absent. There is obviously no mimicry of *H. melpomene* in the first section; neither can its occurrence, so far as concerns the upper-side, be reasonably claimed in the second. For although the red bar in the fore-wing may be urged as a mimetic character, this is rendered highly improbable by the presence of the striking basal pale marking, which, with the black ground-colour, gives the insects a totally different appearance. It is only in the third section that we find any real mimicry, namely, in the females of *charops*, *venezuelana* and *peruviana*, the last two being probably only local races of the first. These forms being brown and having lost all traces of the pale suffusion, do very convincingly suggest the existence of a close mimetic association with *H. melpomene*. Here, if anywhere, there should be evidence of reciprocal mimicry; but unfortunately for the hypothesis *charops* happens to be one of the species of *Pereute* which does not possess any red spots at all on the under-side, and this fact alone renders it highly improbable that the spots of *melpomene* are diaposematic. It appears even open to doubt whether they have any real mimetic value at all. In *Pereute* they occur most markedly in the more primitive, and apparently non-mimetic, *telthusa*, and yet they have actually been lost in *P. charops*, although it closely mimics a *Heliconius* in which they are present. How then can we consider that these spots are so important that they have been modified in *melpomene* by the influence of the very different *P. leucodrosime* (belonging to section 2), especially when it is noted that they differ considerably both in number and position in the two species? Further, if their mimetic value is so

great, how can we explain their absence in *P. callinice* which in other respects so closely resembles *P. leucodrosime*? A general contemplation of all the facts must, I think, inevitably lead to the conclusion that these red spots have been quite independently developed in *Heliconius* and without any Pierine influence whatever.

II. *The under-side red spots in the Pierine, Archonias tereas, and Papilio zacyanthus.*

This case was originally put forward in conjunction with the preceding one, and will be found under the same references. For various reasons it is advisable to treat it separately. The line of argument in favour of Diaposematism is quite similar, it being contended that though the Pierine has evidently mimicked the Papilio in all its principal characters, yet in the case of the red spotting of the under-side the influence has been in an opposite direction.

We may first consider the red markings in *Archonias*. The genus falls into four sections, so far as mere pattern is concerned. The first section comprises a single species, *theano*, which evidently represents the more primitive colouring of the genus. Its upper-side is dark brown, with vague whitish markings, while the under-side presents a very characteristically Pierine appearance, being yellowish or whitish with a broad white-spotted dark border and the nervules broadly darkened; a colour scheme which continually reasserts itself in various genera of Pierinæ in all parts of the world; finally the basal red spots are conspicuous by their absence. The second section contains species which mimic various Ithomiinæ, and in all of them the red spots are wanting. The species of the third section mimic certain *Aristolochia* Papilios and these gradually merge into the fourth section which has developed *Heliconius*-like colours. In these last two sections the species all exhibit two red basal spots below, though these differ in position from those of *Pereute*. In the latter the spots are situated obviously on the wing, while in *Archonias* they are placed on the extreme edge of the base and on that portion which is bent against the thorax, so that they appear, unless closely examined, to be

actually on the thorax itself. When we turn to *P. zacyanthus* and its allies we find that they have no red spots on the wing, but only on the thorax; a condition which is highly characteristic of *Papilio*, but which never occurs, so far as I am aware, in any Pierine. At first sight it might appear as if this furnished good evidence as to *Archonias* having mimicked the *Papilio* in this respect, especially as the most primitive species has no red spots at all. But this view is rendered less probable by the occurrence of similarly placed markings in various non-mimetic species of *Catantixia* and other closely allied Pierine genera. On the other hand, Dr. Dixey advocates the opposite view, namely, that the Pierine has influenced the *Papilio*. But a consideration of the prevalence of these red spots in the latter genus shows that this suggestion is even less probable than the other.

In Rothschild and Jordan's revision of the American *Papilios* (Nov. Zool., 1906, p. 435) these insects are divided into three sections. The first of these, the *Aristolochia* *Papilios*, again fall into four groups. Now the first three groups contain no less than 45 species every one of which has thoracic spots like those of *P. zacyanthus* (which belongs to the third group), although many of the species have no mimetic relations with any Pierines. In the fourth group the red spots are replaced by yellow or white, except in the case of *polydamus* and its numerous races, in which the spots are red and there is in addition a red spot at the base of the hind-wing. Again, basal red-spots on the hind-wing are to be found in a considerable number of American *Papilios* belonging to Section III, in which there can be no question of Pierine influence. If we turn to the East we find a precisely similar state of affairs, namely, numerous species of quite differently coloured *Papilios*, including most of the splendid *Ornithopteras*, which have developed either red spots on the thorax, or on the base of the hind-wing (sometimes to a very remarkable extent), or on both. He who will be at the pains to investigate these facts for himself must, I think, unhesitatingly reject any argument for *Diaposematism* in this particular instance. The evidence in favour of an entirely independent development by the *Papilios* of these distinctive markings appears to be overwhelming.

III. *Why do both sexes of Archonias tereas mimic only the female of Papilio zacynthus?*

A second argument for Diaposematism has been based on these same two species, considered from a somewhat different standpoint. The case was stated as follows: "So far as I am aware no explanation has yet been offered of the fact that it is the females and not the males of *Papilio polymetus*, *P. zacynthus*, etc., that are resembled by *Eutерpe tereas* and *E. critias*; whereas the males, which display brighter colours, afford at least as good, if not better, models for imitation. I would suggest that this is really due to 'reciprocal mimicry.' The protection gained by the resemblance between the Pierines and the Papilios is not all on the side of the Pierines, but mutual; and the female Papilios have, as is usual, felt the need of it more urgently than the males. For this reason the female Papilios have been led to meet the Pierines by discarding, or at any rate by not adopting, the bright metallic-blues and greens that ornament the other sex." (Trans. Ent. Soc. 1894, p. 298, note.)

The colour of the ♂ *P. zacynthus* differs principally from that of the ♀ in that the posterior two-thirds of the fore-wing patch is covered with metallic-green or blue scales, only the anterior portion being white; whereas in the ♀ the whole patch is white. The contention for reciprocal mimicry here centres entirely on the supposition that it is difficult otherwise to explain why the *Archonias* have not acquired the metallic patches of the male Papilios. In considering this difficulty the first point which suggests itself is to examine the occurrence of metallic colours in other American Pierines. This inquiry reveals the interesting fact that not a single one of these has developed any metallic colours. The same limitation holds good in Asia, as Wallace long ago pointed out, in his classical paper on the Eastern Pierines: "The metallic blue of *Morpho* and of the Lycænidae, and the rich green of various shades which occurs in most other groups of butterflies are entirely absent" (Trans. Ent. Soc., 1867, p. 301). In fact, so far as I have been able to ascertain, it is only in Africa that any Pierines have developed such metallic scaling, and there it is confined to the males of only two or three species of *Teracolus*. But I cannot find that any Pierine mimic has ever produced this type of

colouring. In these circumstances the supposed difficulty in regard to *Archonias* evidently vanishes. It is no longer remarkable that it has not developed the metallic effects of the ♂ *Papilio*; indeed it would be much more remarkable if it had actually done so. The mimicry has simply followed the line of least resistance, and is in every way consistent with the interpretation of a simple Müllerian approach. It is possible that a fuller knowledge of the habits of the insects would throw more light on the matter; for I note that Wallace mentions that in several species of this group of *Papilio* the sexes do not inhabit the same stations (Trans. Ent. Soc. II, 1854, p. 255).

Another point raised by Dr. Dixey, in support of his interpretation that the *Papilio* has been influenced by the Pierine, is Müller's statement (Proc. Ent. Soc. 1879, p. xxiv) that in the Santa Catharina district of Brazil *Pap. nephalion*, which there represents the model, was comparatively scarce while *Arch. tereas* was common. But in the same paper (p. xxv) Müller has expressly uttered a warning against any such deduction from his statement: 'Thus the black *Archonias tereas*, with the white spots on the margin of the fore-wings and the rose-red of the hind-wings, presents a strange appearance among its congeners, whilst *Papilio nephalion* belongs to a long series of similarly coloured species, so that where this *Papilio* is rare and the *Archonias* common, we cannot for this reason regard the latter as the model of the former.' Unfortunately Müller does not mention whether he had observed any other species of the numerous *zacynthus*-like *Papilios* in Santa Catharina, for this would be of great importance in interpreting the facts. It remains however that all local observers are agreed that the type of colouring exhibited by *zacynthus* is the most characteristic, abundant and dominant *Papilio* pattern in Brazil, and perhaps in Tropical America; nor do any species which I have seen show the least sign of having been influenced by *Archonias*. It may be noted that the mimetic forms of these Pierines persistently retain a characteristic *Archonias* marking, namely, a pale costal streak on the under-side of the hind-wing. Now, if they had really exercised a strong influence on the colouring of the *Papilios* as suggested, it seems only reasonable to suppose that we should find some effect produced by this characteristic stripe. But no trace of it can be seen either in *P. nephalion* or any other species of the

æneas and *lysander* groups that I have examined. Finally, there does not seem any reason to suppose that in these Papilios the females represent a modification of the male colouring. On the contrary, it appears far more probable that the female pattern is the older, and that the metallic patches of the males are a later development; indeed there are several allied species in which they are non-existent.

IV. *The suggested reciprocal resemblance between Pieris locusta and Heliconius cydno galanthus.*

In Trans. Ent. Soc. 1896, p. 72 (note), Dr. Dixey suggested tentatively that *P. locusta* ♂ was a mimic of *Heliconius melpomene*, so far as the under-side of the hind-wing was concerned. In Trans. Ent. Soc. 1897, p. 325, this idea was abandoned, and the very different *H. cydno galanthus* was then definitely proposed as the model. The resemblance however is certainly not of a kind to carry general conviction. The most characteristic feature of the under-side of the *Heliconius* consists of two curved chestnut stripes right across the hind-wing, having their origin at the middle of the inner margin. There is no trace of this marking in *P. locusta*, nor, so far as I am aware, does it occur independently in any American Pierines, although its appearance is simulated in several mimetic species by a prolongation of the lowest basal red spot. But the main point at issue is the contention that "there is more reason to suppose that the *Heliconius* has adopted certain features from the *Pieris* (for example, the whiteness of the ground-colour, and the disposition, if not the existence, of the basal red marks) than that the converse alone has taken place" (*l. c.* p. 327). The reasons in support of this belief are not mentioned, but we have seen above that the contention that the red basal spots have been produced, or even materially affected, in *Heliconius* by Pierine influence cannot be reasonably sustained. It remains only to deal with the proposition that the white area on the under-side of the fore-wing in the *Heliconius* must be explained by its having directly mimicked the Pierine. Now the very position of this white patch is of itself a serious difficulty in the way of such an interpretation. The marking can have no significance during flight, for on its upper-side *P. locusta* ♂ has not the slightest resemblance to the

Heliconius, being an ordinary plain white insect with a moderate black border. On the other hand, in a position of rest this marking would be concealed, and it is therefore difficult to understand what mimetic value it could have. But it is only fair to point out that when the above proposal was made the true ♀ of *P. locusta* was not known, the ♀ figured by Dr. Dixey (*l. c.* Pl. VII, fig. 7) belonging really to *P. tithoreides*, Butl. Now the real ♀ of *locusta*, which is evidently a rare insect, does present a fair general resemblance on the upper-side to *H. c. galanthus*. For the whole of the hind-wing and the basal part of the fore-wing have been very much darkened and thus present a likeness to the similar dark blue areas in the *Heliconius*. We need not therefore labour the point as to the mimicry of *locusta* ♂, but may merely consider whether it is reasonable to suppose that the white patch on the upper-side of the fore-wing of *H. cydno* and its numerous varieties has been produced by their directly mimicking *locusta* ♀.

The first point is the question of unpalatability. In the cases previously discussed there do appear to have been reasonable grounds for suggesting that the Pierines involved were distasteful. Here there appears to be none. Thus *à priori* it seems extremely doubtful that a scarce ♀ Pierine, of questionable unpalatability, should have been able to profoundly modify the colouring of both sexes of an undoubtedly nauseous and abundant species such as *H. cydno*. The crux of the whole argument lies in the assumption that white colouring is abnormal in *Heliconius* and must therefore be due to Pierine influence. Now Riffarth and Stichel recognise 9 sub-species and 5 subsidiary forms of *cydno*. Of these 7 have a conspicuous broad white border in the hind-wing; 3 have this border of a yellow colour, and 4 (including *galanthus*) have no distinct border at all. It seems probable that the borderless *galanthus*-like forms represent the older type, of which the much commoner pale-margined forms are a more recent development. The hind-wings of these latter insects are quite different from anything to be found among American Pierines, and it can scarcely be contested that these broad white margins have been developed by *Heliconius cydno* and *sapho* quite apart from Pierine mimicry; and they have again been independently produced in the very different *H. cyrba*. Further we may note that in Guiana *H. hecale* presents a large white area in the fore-wing;

while other species of this inordinately variable genus exhibit forms having white patches or bands in the fore-wing. Of these may be mentioned various forms of *sapho*, *xenoclea-notabilis*, *anderida-albicilla*, *antiochus-antiochus*, *wallacei-wallacei* f. *elsa*, *wallacei-colon* f. *clytia*, etc., while in such forms as *doris-doris* and *erato-erato* f. *udalbrica* the conversion of the yellow discal patch into white crops out as an occasional variation, thus showing an inherent tendency in that direction.

There seem therefore no real grounds for believing that *Heliconius* cannot develop white markings, except under pressure of external mimetic influence, and the most satisfactory interpretation of the present case is that the ♀ *Pieris* is a simple Batesian mimic of the *Heliconius*.

V. *The suggested reciprocal resemblance between the African Papilios of the zenobia group and the Aeraeinae genus Planema.*

The normal upper-side colouring of the Papilios of the *zenobia* group may be briefly described as black, with a continuous whitish or yellowish oblique stripe across both wings, which varies in width, and often becomes macular in the fore-wing. There are 12 species recognised by Aurivillius, of which 5 present this type of colouring in both sexes, while in the remaining 7 the female is mimetic of either a *Planema* or an *Amauris* of the *echeia* pattern. In both sexes of all the species there is on the under-side of the hind-wing a large basal triangle of a golden-brown or chocolate-brown colour. In the largest species, such as *cypræofila* and *gallienus*, in which the females are non-mimetic, this triangle attains its greatest size, and is traversed by continuous black inter-nervular streaks. In the mimetic species, as well as the non-mimetic *zenobia*, the streak nearest the costa is broadly divided so as to form two spots. In the females of the mimetic section the brown area is more reduced, causing a considerable shortening of the black streaks nearer the inner margin, and thus producing a more spot-like appearance. In this condition the marking presents an obvious superficial resemblance to the brown, black-spotted area which is found on the hind-wings of so many Planemas. This resemblance has been generally explained as being due to the Papilios being Batesian mimics of the Planemas,

whose unpalatability is well established; a view which is still strongly held by Mr. Trimen. But this idea has been traversed by Prof. Poulton (Trans. Ent. Soc. 1902, p. 488), who claims that the brown triangle is more characteristic of, and more highly developed in, the *Papilios* than the *Planemas*. He therefore assumes the *Papilios* to be unpalatable, and suggests that it is their mimetic influence which has produced the brown triangle in *Planema*; and then subsequently the process has been reversed and the *Papilios* have begun to mimic the *Planemas* by a partial conversion of their stripes into spots, this being described as "a late diaposematic response" (*l. c.* p. 489).

Although this suggestion is supposed to indicate a case of diaposematism, it is clear that the interpretation is not really diaposematic, in the sense of suggesting a mutual simultaneous approach. On the contrary, it evidently comes under the heading of what I have termed (p. 103) Alternating Resemblance, and involves the assumption of a corresponding alternation in the individual numbers of the respective species.

The main point at issue is whether these *Papilios* are really unpalatable, and of this there is no practical evidence. It can only be settled by direct experiment, and by careful observation of the insects in relation to their environment. Personally, I have had experience of only a single species of the group, namely, the extremely local *P. echerioides*. The general behaviour of this insect appears to me to be entirely at variance with the supposition that it is endowed with nauseous qualities, but its habits suggest a possible interpretation of the facts under discussion. In South Africa *P. echerioides* is essentially a forest insect; it is not to be found in open woodlands, but only among dense and heavy timber, coursing irregularly over the undergrowth beneath the trees. In such an environment, lit up by splashes of broken sunlight, the under-surface of the butterfly, as it settles on some low shrub or among dead leaves on the ground, exhibits none of the conspicuous warning characters which have been attributed to it; on the contrary, its colours harmonise most effectively with the surroundings in which it spends most of its time and in which it habitually goes to rest.

The habits of our only *Planema*, *P. aganice*, are very different. For although it is also a lover of forests, it does not fly beneath the trees, but is to be found sailing about

the clearings round the edges of the forest patches; and when it settles there is no attempt at concealment, but it hangs limply from the end of a leaf or bare twig in the full sunlight. In such circumstances the same colour scheme, which in the *Papilio* makes for concealment, becomes conspicuous and obtrusive. But it may be asked, if their habits are so different, how can it benefit the *Papilio* to mimic the *Planema*? The question of food-supply furnishes the answer. In the forest itself flowers are few and far between; they are lovers of sunlight and are to be found principally in the clearings and round the edges of the forest. To such places the *Papilio* resorts to feed; it is here that it comes into contact with the *Planema*; it is here that the forces which make for mimicry find scope to operate.

There seems reason to believe that the Central and West African Papilios of this group have habits similar to those of *echerioides*. The group has probably originated in West Africa and spread thence East and South. The larger species, *cypræofila* and *galliensus*, with non-mimetic females, appear to be the least modified members of it, judging by their outline and colouring. The large brown triangle of these species, with its unaltered *Papilio* streaks, may then represent a scheme of *cryptic* coloration independently evolved by the group. The roughly *Planema*-like appearance of this pattern would of itself determine a mimicry of *Planema* wherever any species of the group came into special contact with that genus. The resemblance would be enhanced by the breaking of the stripes into spots, and by the reduction in size of the brown triangle, so that it would become, as we see it, smaller in the mimetic female than in its non-mimetic male. That this progressive diminution has actually taken place seems to be confirmed by a very interesting form of *Papilio cynorta* from Uganda, recently described by Mr. Neave under the name *peculiaris* (Nov. Zool. XI, p. 342, Pl. I, f. 7). According to Dr. Jordan (Trans. Ent. Soc. 1906, p. 219, note) the males are hardly distinguishable from the typical Western *cynorta*. But whereas the female of that form mimics *Planema gea*, and has a conspicuous brown triangle, *peculiaris* mimics *Pl. paragea*, in which the basal triangle is almost obsolete. As a result we find that in the *Papilio* the triangle has been reduced to very small dimensions, all the stripes have disappeared

from it and only the round spot above the cell is left. Here, at least, it is clear that, so far as concerns the brown patch, it is not the *Papilio* which has influenced the *Planema*, but *vice versa*.

A final point may be noticed. On the West Coast the genus *Planema* attains its greatest development and the *echeria* type of *Amauris* is absent; the mimetic *zenobia* *Papilios* therefore all mimic *Planema*. In East and South Africa where *A. echeria* and *albimaculata* occur with *Planema*, the *Papilios* have abandoned the latter and mimic the *Amauris*; the reason being, no doubt, that the *Amauris* are much less particular as to the stations which they frequent and are to be found commonly flying right in the shady forests where the *Papilios* live. The facts appear to fully support Mr. Trimen's view that with these *Papilios* the earlier tendency was to mimic *Planema* and that they have later been diverted towards *Amauris* (cf. Trans. Ent. Soc. 1902, p. 488).

VI. *The suggested diaposematic resemblance between the two Eastern Pierines Huphina corva and Ixias baliensis, ♀.*

This suggestion was made by Dr. Dixey in a short paper in Trans. Ent. Soc. 1906 (p. 521, Pl. XXXI). He there calls attention to the fact that *H. nerissa corva* differs from the typical *nerissa* of Continental India in the greater width of the black border on the hind-wings. This it is suggested is a mimetic approach towards the ♀ of *Ixias baliensis*, which is only a slight local modification of *I. reinwardtii*. But so far as concerns the fore-wings, *I. baliensis* has departed from the normal colouring of ♀ *Ixias* by the development of a row of four whitish sub-marginal spots in the apical black area. In this case it is claimed that the *Ixias* has mimicked the *Huphina*, so that there has been a reciprocal mimetic interchange.

This interpretation involves the assumption of unpalatability in both the species. My friends, Colonel C. T. Bingham, Colonel N. Manders and Mr. R. Shelford, who are all acquainted with both genera in the field, inform me that while the *Huphinas* certainly exhibit a slow flight and a general demeanour which would suggest the possession of unpleasant qualities, such is by no means the case with the species of *Ixias*, which are active and wary insects. This fact, taken in conjunction with the obviously procrystic

under-side colouring which prevails in that section of the genus to which *I. baliensis* belongs, renders it very improbable that the *Ixias* has in any way influenced the *Huphina*. Furthermore, so far as the ♀ sex is concerned, the increase of the black border in the hind-wing of *H. nerissa corva* is not particularly striking, and there are two females in the British Museum which in this respect are scarcely to be distinguished from a ♀ *nerissa* from Sikkim. It is in the ♂ that the increase is specially noticeable, and this sex can certainly not be reasonably regarded as a mimic of *I. baliensis* ♀, for the entire absence of the heavy black bar across the cell of the fore-wing gives it a very different appearance.

Another serious difficulty, to which Dr. Dixey has himself referred, is the discrepancy in the geographical range of the two species. To meet this it is suggested that either *H. corva* has extended its range, or *I. baliensis* has contracted its range, subsequently to the production of the mimicry. The facts do not appear to justify either of these assumptions. Dealing first with the *Huphina*, we find that the continental form *nerissa* (with its var. *phryne*) is represented in the Andamans by a slightly darker form, *lichenosa*, leading up to the broad-bordered race *corva* (including the scarcely separable *sumatrana*) which is found throughout Sumatra, Java and up to the islands of Bali and Lombok. On the other hand, so far as we know at present, the range of *Ixias reinwardtii* lies entirely to the east of this, namely, in the islands of Timor, Flores, Sumba, Sumbawa, Lombok, up to Bali, which constitutes its westernmost limit.

If we assume *H. corva* to be a mimetic modification of *nerissa* which was evolved in the island of Bali and has since extended thence, we must suppose that originally typical *nerissa* occurred throughout Sumatra, Java and Bali. If this were so, why should *corva* have so totally replaced *nerissa* in Java and Sumatra, where *Ixias baliensis* does not occur, and how are we to explain the existence of an intermediate form in the Andamans? On the other hand, there is even more difficulty in accepting the supposition that *I. reinwardtii baliensis*, which is confined to a little island some 80 by 50 miles in extent, should have originally ranged throughout Java and Sumatra (with a combined length of some 1,700 miles), from which it has now completely disappeared. For the

slight characteristics which distinguish *baliensis* from the typical race *reinwardtii* are essentially such as we should expect to find in a group of individuals which have been comparatively recently isolated from the main body of the species; in other words, *baliensis* differs from *reinwardtii* simply because it has been confined to the island of Bali.

If we examine such a series of forms as *Huphina phryne*, *nerissa*, *lichenosa* and *corva*, it seems clear that we are dealing with those progressive modifications which are generally comprised under the name of geographical races; that is to say, the differences exhibited are accepted as due to the influence of either climatic causes, or isolation, or a combination of both. It is the more probable that such is here the case when we find that the allied Indian *H. nadina* ♂ presents similar modifications; being represented by an intermediate form, *andamana*, in the Andamans, and a more heavily-bordered form, *fawcetti*, in Sumatra. Such progressive widening of the black borders may also be observed in other Pierine genera, such as *Delias*, *Prioneris*, *Appias*, etc.; while from Africa, and doubtless from many other parts of the world, numerous parallel cases could be cited in which no mimetic interpretation could cover the facts.

Further, it may be mentioned that heavy black borders are a very common feature in the genus *Huphina* and exist in a majority of the species occurring in the Malay Archipelago. They attain their highest development in *affinis* (Celebes), in which they occupy nearly half the wing and are far broader than anything to be found throughout the whole genus *Ixias*. A considerable number of species from these islands could be mentioned in which the borders are markedly better developed than in *H. corva*.

I find myself unable therefore to accept the suggestion that the broader black margin of *H. corva* is due to the direct mimetic influence of *I. baliensis* ♀. It is possible that the *Ixias* may have mimicked the *Huphina*, but in dealing with such black and white Pierines a hasty assumption of mimicry is specially to be deprecated; and it is well to bear in mind the judicious warning in this connection uttered by Wallace forty years ago: "By far the most general type of colouring in the Pieridæ, and which recurs in hundreds of species, is a white ground with a black outer border, always most developed at the

apex of the upper-wings, and very frequently less marked on the hind-wings. It is not therefore surprising that among the many slight modifications of this commonest and most simple type of coloration, two species belonging to different genera should closely resemble each other externally" (Trans. Ent. Soc. 1867, p. 311).

Finally, it may be mentioned that very little is known about the ♀ of *I. baliensis*. This sex was not known to Frühstorffer when he described the subspecies in 1897. There is a single specimen at Oxford, namely, that captured by Mr. Shelford and figured by Dr. Dixey (*l.c.*), and only one in the British Museum. The latter differs considerably in appearance from the Oxford ♀, in that it has a pronounced suffusion of yellow in the fore-wing and a reduction of the black markings; it can in no sense be regarded as a mimic of *H. corva*. There is no evidence available as to the relative occurrence of these two forms.

VII. *The suggested reciprocal mimicry between Papilio dardanus ♀ form cenea and the Danaïnes Amauris echeria and albimaculata.*

The remarkable suggestion that these two dominant species of *Amauris* have been modified in mimicry of *P. dardanus* was propounded by Professor Poulton in Trans. Ent. Soc. 1906, p. 292, and the following comments will be better understood if reference be made to the numerous plates with which his paper is illustrated.

On examining some of the more primitive females of *P. dardanus* (such as *trimeni*, *l.c.* Pl. XVIII, fig. 1), Professor Poulton was struck by the outward production of the basal pale patch of the hind-wing between veins 5 and 6, a character which is readily recognisable in the non-mimetic ♂. Now, in *Amauris echeria* and *albimaculata* the discal pale patch also shows a very marked external angulation at about the same position; but it is contended that this form of marking cannot have been acquired from the *Amauris* by the *Papilio*, because it is ancestral in the latter species. The conclusion is therefore reached that the *Amauris* must have acquired it by mimicking the *Papilio*, and subsequently exaggerated the character. The possibility of independent origin is not considered.

This suggestion invites criticism along three lines: the question of the edibility of the *Papilio*; the relative

numbers of model and mimic; and an examination of the occurrence of the angular markings in the species allied to the *Amauris* and *Papilio* respectively.

With regard to the inedibility of *dardanus*, unfortunately no experiments have been made with this species,* although Mr. Mansel Weale has observed the ♂ to be captured and eaten by a flycatcher (*Terpsiphone perspicillata*) in Cape Colony (Proc. Ent. Soc. 1874, p. 132). But my own observations of the general habits of the species in its natural haunts cannot permit me to regard it as an unpalatable insect, as I should apply that term to an *Acræa*, *Mylothris* or *Neptis*; and that very accurate observer, Mr. R. Trimen, F.R.S., informs me that he is strongly of the same opinion. He was particularly impressed by the fact that the ♀ shows a persistent habit of concealing itself beneath the herbage when not actually searching for food; a habit also noted by the late Colonel Bowker and Mr. Mansel Weale. This behaviour is in striking contrast to that of all S. African species having undoubted nauseous qualities. Again, no one who has seen the ♂ *dardanus* at rest can doubt the cryptic value of its under-side colouring, and Mr. Trimen has quoted an observation of the late Mrs. Barber showing the care exercised in selecting a suitable resting-place (S. Afr. Butt.; iii, p. 254),† another habit which is quite at variance with the assumption of inedibility. Finally, when we examine the more primitive and non-mimetic females of the Abyssinian *P. antinorii* and the Madagascan *P. meriones*, from which *dardanus* is derived, we find that their under-sides are also thoroughly cryptic in character. Thus the balance of evidence certainly appears to be against the supposition

* Drs. Dixey and Longstaff record that the ♂ had a similar smell to that found in *P. demodocus* and described as "like fusty packing-straw," but in *dardanus* it was "less musty." The ♀ was not investigated, so that it is not certain that this odour may not be merely sexual in character, like the musky odour of male hawk-moths mentioned by Darwin ("Descent of Man," p. 308). It may be noted however that a ♂ *Pap. leonidas* examined by Dr. Dixey was considered to have the unpleasant smell of *D. chrysippus*; whereas several males smelt by Dr. Longstaff were found to give a "strong, sweet, 'white flower' scent, followed by something more spicy." A similar discrepancy occurs in their records as to *Neptis agatha* (Proc. Ent. Soc. 1906, p. v). The exact significance of the observations therefore remains doubtful.

† A similar observation has been made by Surgeon-Major Clements at Sierra Leone (cf. Proc. Ent. Soc. 1906, p. xxix).

that *dardanus* possesses nauseous qualities; and if this be so, the argument for Diaposematism falls to the ground.

It is not always easy to form a definite conclusion as to the relative numbers of a model and its mimic, but there can be little chance of error in the present instance. We may first note that if the ♀ *dardanus* exhibits this angular marking in such of its forms as *hippococonoides* or *trophonius*, this can have no mimetic influence upon *A. echeria*, because those forms do not at all resemble this species, but mimic two other Danaines. For this reason we must only consider the occurrence of this angulation in the *cenea* form which mimics *echeria*. We shall find however that that character occurs more rarely in *cenea* than in the above forms, and then nearly always in the examples which are least like *echeria*. Therefore in estimating numbers, we have on one side a comparatively rare variation of a single form of only one sex of the *Papilio*, and on the other side both sexes of two very common species of *Amauris*. From what I know of the prevalence of these two insects in nature it would be a conservative estimate to reckon that the latter would exceed the former in the ratio of 100 to 1. It has already been shown how impossible it is to believe that in such circumstances the mere operation of the Müllerian factor could have compelled the *Amauris* to mimic this variation of the *Papilio*. Here again the facts appear to entirely forbid a diaposematic interpretation.

When we investigate the occurrence of this angular marking in other species of *Amauris* and *Papilio*, still further difficulties present themselves. With one or two exceptions all the species of *Amauris* have a large basal or sub-basal pale patch on the hind-wings. Out of 20 of such species I find that no less than 13 possess the angulation in question. In *psyttalea* and *dominicanus* it is variable in its occurrence; in such forms as *lobengula* and *crawshayi* it is very similar to what we find in *Pap. dardanus*; in *ochleides*, *hyalites*, etc., it is more marked; whilst in *echeria* and *albimaculata* it is far more developed than in any *Papilio*. On the other hand, this character is a very unusual one in the genus *Papilio*; indeed I have failed to find anything which is really comparable with the *Amauris* pattern except among those *Papilios* which tend to mimic Danaines in which it already exists. These facts, again, are quite at variance with what

we should expect to find if the argument for reciprocal influence were sound.

It is by no means evident that this angular marking has any real mimetic significance at all. In the more primitive and non-mimetic ♀♀ of *Pap. meriones* and *antinorii* the hind-wing is usually pale yellow, with three large, disconnected, submarginal black patches. The first step in the mimetic approach towards the Danaines appears to have consisted in the linking up of these patches to form the continuous dark border so characteristic of the models. An examination of the various forms of the ♂ *dardanus* shows that the costal and median black patches usually unite in a very characteristic manner, so as to give rise to the angulation in question; and we may reasonably assume that a somewhat similar process took place in the females. Now, it will be found that the development of the angle is fairly constantly correlated with a comparatively narrow black border, and therefore it occurs most frequently in the more primitive and less specialised mimics, such as the forms *trimeni* and *hippococonoides*, in which the border is not broad. On the other hand, as the inner edge of the border tends to approach the apex of the discoidal cell, so does the angle become more or less completely obliterated. In *Amauris echeria* and *albimaculata* the black border is very broad, and it will be found that the specimens of *P. dardanus* f. *cecea* which present the closest resemblance to them are those in which the border is very broad and the angle consequently obliterated (cf. Trans. Ent. Soc. 1906, Pl. XVII, figs. 8-10, as against fig. 11, which is a comparatively poor mimic).

So far therefore from being able to accept the suggestion that the angular marking has been produced in the *Amauris* by the influence of the *Papilio*, it appears to me that this merely transitional character in the *Papilio* has had so little mimetic value that it is actually in process of being eliminated by the influence of the *Amauris*.*

* It is interesting to note in this connection that neither *Papilio echerioides* nor *P. jacksoni* has developed this angulation, although they are excellent mimics of the same two species of *Amauris*.

VIII. *The mimetic relationship between the Danaine Melinda formosa and Papilio rex.*

This point has been discussed by Mr. S. A. Neave in Trans. Ent. Soc. 1906, p. 216 (*cf.* Pl. XI and XII), where he advances the proposition that *Pap. rex* and its local race, *mimeticus*, are not Batesian mimics of *Melinda formosa* and *mercedonia* respectively, but that they are themselves unpalatable insects, which have in some respects mimicked the Danaines, in others served as models for them.

There is no tangible evidence as to the existence of nauseous qualities in these Papilios; it is merely deduced from the supposed reciprocal nature of the mimicry. According to our present knowledge these are very much rarer than the Melindas; indeed, in the case of *mimeticus*, I am not aware of the existence of any specimens beyond the unique type from Uganda, although its suggested mimic is stated by Mr. Neave to be common in that district, and is also recorded from a good many localities in German East Africa.

The foundation of Mr. Neave's argument consists in the assumption that the three species of the African group, or sub-genus, *Melinda*, have been directly derived from *Tirumala petiverana*, which is the African representative of the two common Asiatic species *T. limniace* and *septentrionis*.

Now, the Melindas differ from *petiverana* in having the fore-wings considerably more elongated, and also in having the pale markings at the base of the hind-wing more consolidated, so as to form a continuous pale area, interrupted only by the darkened nervures. These are therefore stated to be "new developments and non-ancestral characters" which have been acquired by the Danaines from *Papilio rex*.

But the validity of this suggested genealogy seems open to serious doubt. The fact that *T. petiverana* represents merely a recent modification of some Eastern *Tirumala* is so clear that it is generally treated as only a local race of *T. limniace*. On the other hand, the Melindas differ from the true Tirumalas not only in the structure of the ♂ brand (upon which Moore founded his genus), but also in several characters in the ♂ genitalia, as well as their general facies. There is no species of *Melinda* in Asia, and these differences appear to indicate that the African forms have been isolated

for a very considerable time from the Eastern Tirumalas. We have therefore no reason for assuming that the obviously recent intruder, *T. petiverana*, must have been the direct progenitor of the Melindas.

The more recent intrusion of *petiverana* must also be inferred if we apply Professor Poulton's test, namely, a comparison of the mimetic effect produced by the respective forms. In spite of its abundance and widespread occurrence in Tropical Africa *petiverana* has not yet succeeded in producing a really close mimic, though there are two or three species which present a generalised resemblance to it; whereas all three Melindas have entered into a very close mimetic association with some particular species, thus indicating that they have been resident in the country for a longer period.

There seems to be no justification for assuming that *Melinda* has been directly derived from any particular species of Asiatic *Tirumala* as we now know it. But with regard to the pale patch in the hind-wing referred to by Mr. Neave, we may note that it occurs in several Eastern Tirumalas, such as various forms of *limniace* and *melissa*, *choaspes*, etc.; its appearance being very similar to what we find in *M. formosa*. Wherefore the statement that this character must be a "new and non-ancestral development" in the last species cannot be reasonably maintained. Moreover, this type of marking is very common among Asiatic Danaines and is particularly characteristic of the African forms.

As to the pointed fore-wing of *M. formosa*, it is true that no *Tirumala* exhibits a similar shape; but this again is far from being an unusual character among Eastern Danaines, and in the genus *Nasuna* it has attained an even greater development than in *Melinda*. An elongated fore-wing is also a very common feature among the African species and is to be found in a considerable number of *Amauris*. It is by no means clear why these slow-flying butterflies should have so largely adopted this pointed form of wing; but it seems not improbable that the cause which has produced this effect in *Amauris* has also operated on the Melindas during their prolonged isolation from their Eastern progenitors. This view is indirectly supported by the following facts.

Mr. Neave has pointed out that in the Abyssinian subspecies *M. formosa neumanni* the fore-wings are slightly

shorter than in the typical form. This is exactly paralleled in the Abyssinian *Amauris hecate strictica*, which has the fore-wing very distinctly shorter than in the Western *hecate*; and again examples of *A. echeria streckeri* from the same locality have these wings appreciably less pointed than in *A. echeria jacksoni* from British East Africa. Neither can there be any question as to mimetic influence between these three very different species. We are therefore justified in assuming provisionally that the shape of the wing is affected by some general local factor.*

It has been suggested by Mr. Neave that *M. formosa neumanni* represents an intermediate stage between *M. formosa* and *T. ptyverana*; but he then had only a single example of *neumanni* at his disposal. Dr. Jordan has very kindly brought up to London for my examination three typical specimens of this Abyssinian form, and he entirely agrees with me that there are no adequate reasons for accepting this suggestion, the improbability of which has already been shown on other grounds.

The attempt to interpret the mimicry in this case as being reciprocal does not appear convincing, while the facts are entirely consonant with the conception that the *Papilio* is a simple Batesian mimic of the *Melinda*. *P. rex* is a very isolated species and has evidently been profoundly modified by mimetic influences. But its structural characters, in conjunction with the characteristic arrangement of the submarginal row of yellow spots, indicate that its nearest ally is *P. demodocus*, which has the fore-wings much less produced. It is probable therefore that *rex* represents a mimetic modification of some *demodocus*-like ancestor.

My friend Mr. Trimen has kindly permitted me to quote the following comments which he has sent me in connection with this case: "The latter feature [elongation of fore-wing] strikes me as affording extremely weak support to that theory [reciprocal mimicry], seeing that, next to the showy and strongly-contrasted colours on both upper and under surfaces of the wings, there is no feature so

* Wallace has recorded ("Malay Archip." p. 215) that there is a similar tendency in the Island of Celebes for butterflies of different genera and subfamilies to develop a markedly pointed or elongated wing. It may be noted that *Amauris comorana*, in the Comoro Islands, has a sharper fore-wing than any continental species, being in this respect very similar to *M. formosa*.

universally and saliently denoting the unpalatable groups of butterflies. It is impossible to doubt that in all these groups the advantage of the prolongation of the fore-wings is primarily to increase conspicuousness by that special form of wing, and secondly to increase the area available for warning colours. The character being so general and so fixed in tendency, one cannot be surprised to find some species developing it more than others; and there seems no need, in such a case as that of the *Melinda* Danaines, to have recourse to the far-fetched idea of these abundant and distasteful butterflies having to borrow so natural a feature from the rare *Papilio rex* and extremely rare *P. mimeticus*. In the genus *Acræa* no one deems it necessary to account for such great prolongation of the fore-wing as is found in *A. perenna* or *A. pharsalus* by assigning it to mimicry of any butterfly of a remote family."

These then are the cases which have so far been adduced to demonstrate the actual occurrence in nature of Reciprocal Mimicry. To my mind, the facts when critically examined do not lend any valid support to such a hypothesis; nor even do they appear to justify in any instance the assumption of that mimetic inter-action which I have termed Alternating Mimicry or Resemblance.

The Scope of Batesian Mimicry.

Up to the present time it has generally been considered that mimicry between two species which both possess distasteful qualities cannot possibly be explained on the lines of Bates' theory, but that the association must be Müllerian in character; in other words, that it can only have been produced by the selective action of experimental tasting by inexperienced animals. Now when I began experimenting on these subjects in South Africa, some twelve years ago, one of the first things that impressed me was the fact that there was clearly a considerable difference in the degrees of distastefulness, not only between different genera of butterflies, but even within the limits of a single genus, such as *Acræa*. Further, the question was complicated by the divergence in the likes and dislikes of various insectivorous animals. No doubt all this has long been recognised; yet in practice, the application of the Müllerian interpretation involves the assumption of a uniform standard

of inedibility, and the complications which would be introduced by inequality in this respect have not been taken into account.

When we recognise however that there actually are varying grades of unpalatability in butterflies, and that certain enemies may adapt themselves to prey on the less protected forms while avoiding those that are most nauseous, it becomes clear that any mimicry which may arise as a result of such selection could not possibly be classed as Müllerian, but would be due to the simple operation of the principle enunciated by Bates, in spite of the fact that the mimic possesses qualities rendering it distasteful to other animals. That there is no inherent improbability in such a supposition is shown by some experiments I made upon a tame ground hornbill (*Bucorax caffer*) in Natal (Trans. Ent. Soc. 1904, p. 347). To this bird, which roamed unconfined, I gave at different times five species of *Acræa* and one of *Planema*, all of which were readily eaten and with evident appreciation; but when a *Danaida chrysippus* was offered to it, it merely crushed the thorax and dropped it at once, a second specimen being treated in a precisely similar manner. Again, through the kindness of Mr. C. F. M. Swynnerton I have obtained proof that wild Bee-eaters will prey upon *Acræas*; there is also some evidence that they avoid *Danaines*. When fuller information is obtained on this point it may be necessary to reconsider the current supposition that the mimicry of *Acræa encedon* for *Danaida chrysippus* is purely Müllerian.

But there is another way in which Batesian mimicry may have arisen among unpalatable butterflies. Professor Poulton long ago pointed out that insectivorous animals which, under normal conditions, would refuse insects having an unpleasant taste, would yet eat them when driven thereto by hunger. If we suppose that in such circumstances a wild bird were compelled to feed upon distasteful insects, upon making experiments it would doubtless find that while some of these were extremely unpleasant, others would be passable. It seems an entirely fair and reasonable supposition to infer that this bird would select the species which were less unpalatable to the exclusion of the others, and if the necessary variations arose, this selection would tend to cause the former to become Batesian mimics of the latter. Such

conditions would be likely to occur very frequently during the dry winter months in South Africa. Here again I find some confirmatory evidence among my experiments (Trans. Ent. Soc. 1902, p. 344). A tame kestrel (*Tinnunculus naumanni*), which had shown pronounced dislike of both *Acræas* and *Danaida chrysippus*, was starved for twenty-four hours. After eating seven palatable butterflies it was given two *Acræas*, which were swallowed whole; then a *D. chrysippus* was offered to it, which was tasted but emphatically rejected, and immediately afterwards three more *Acræas* were swallowed whole. Thus under the stress of hunger the bitter juices of the *Acræas* were disregarded, but the more highly unpleasant flavour of the *Danaide* still remained a deterrent.

From these remarks we see that the interpretation of Batesian mimicry is not to be restricted only to those cases where an edible species mimics an inedible model; but while in Müllerian mimicry the essential condition is a difference in the individual numbers of two inedible species, in Batesian mimicry the essential condition is a difference in the palatability. Both species may be distasteful, but wherever there is scope for preference, there it is possible for Bates' principle to operate. Thus, so far from being able to accept the suggestion that practically all mimicry among butterflies is Müllerian in character, it seems to me that we have not yet begun to appreciate how wide a significance Bates' principle may have. The question is extremely complex, and resolves itself ultimately into a consideration of the mental attitude of insectivorous animals towards their prey. It is even possible for a single species to be at the same time both a Müllerian and a Batesian mimic of one and the same species in relation to the attacks of different enemies. The final decision on these points must rest with the field-observer and experimenter.

On the greater predominance of the factors which make for Batesian mimicry.

There are some general considerations which also appear to negative the supposition that the occurrence of Müllerian mimicry is far in excess of Batesian. It has already been argued (p. 113) that the operation of the Müllerian factor is practically restricted to the breeding season of birds,

etc., while Bates' factor is in force at all times. But if we further consider the life of an individual bird it is apparent that its experimental period is only of short duration, while for the rest of its life its selective action will be simply in a Batesian sense; its increasing experience giving it added efficacy in this direction. As against this view Professor Poulton has urged (Proc. Ent. Soc. 1903, p. ix) that Müllerian selection is probably more keen than it appears; that we must not estimate it by a comparison of the relative numbers of mature and immature enemies at any given time, but that we must remember that there is a considerable elimination of the young of these enemies, so that a large percentage never reaches maturity, and it is apparently assumed that these individuals only operate as Müllerian factors.

Taking the case of birds, which are, almost certainly, the principal agents in the production of mimicry among butterflies, let us examine this matter of the destruction of the young. We have no exact knowledge on the subject at all, but it is reasonable to suppose that the most critical and dangerous period of a young bird's life is during the time when it is a helpless nestling and also for a few days after it has left the nest, while it is still unable to fly properly, to recognise its enemies or to provide itself with food. It is probable, therefore, that by far the greatest destruction of life among young birds will take place between the time when they leave the egg and the time when they are able to fly properly and forage for themselves. But throughout this period young birds do *not* operate as Müllerian factors; such selective influence as they may have upon the insects in their neighbourhood will be exercised entirely through the medium of their parents, and as these latter will be mature and, presumably, experienced birds, their effect will be solely in a Batesian direction. This aspect of the question therefore does not, as it seems to me, add weight to the Müllerian argument, but rather the reverse.

Tenacity of life in unpalatable species.

Many observers have called attention to the fact that various butterflies exhibit a very remarkable tenacity of life, accompanied by a toughness of the integuments. In all these cases the insects belong to genera in which the

existence of nauseous qualities has been well established, and this tenacity does not appear to occur apart from those qualities. The great utility of such a faculty to insects which are liable to be experimentally seized and rejected by enemies is so obvious that its very existence may be taken as good circumstantial evidence that Müller's factor is an objective reality, and not a mere figment of the imagination. But it must not be forgotten that the very efficacy of this characteristic in saving the lives of the insects and enabling them to propagate their kind after experimental attacks (an essential condition for its development) causes it to become a serious check on the production of Müllerian mimicry; for such mimicry can be brought about only by a progressive destruction, or sexual disablement, by experimental tasting, of those individuals of the mimic which do not conform to the mimetic pattern. Wherefore any quality evolved by the species which diminishes this destruction must, so far as it is successful, prevent a mimetic approach. This limitation of Müller's conception does not appear to have been sufficiently taken into account.

Colour as a guide to unpalatability.

Although the existence of displeasing qualities in butterflies is very generally indicated by bright colours on both surfaces of the wings, such is by no means always the case. Among the *Acravinæ*, *Ithomiinæ*, and especially the *Euplaini*, there are many instances of colouring so sombre that were it associated with the requisite pro-cryptic habits it would serve most effectually as a means of concealment. In such instances it is only the slow heavy flight and generally gregarious habits of the insects which cause them to become conspicuous objects; and these peculiarities of manner are to be found in every species whose distastefulness has been satisfactorily demonstrated. On the other hand, there is at present no experimental evidence which clearly proves the existence of inedible qualities in butterflies which exhibit a strong active flight and general wariness of manner, together with obviously pro-cryptic habits. We may of course assume the existence of such qualities, but the value and desirability of such an assumption must remain merely a matter of opinion.

As a result of a good many years' experience of

butterfly life in South Africa I am convinced that we shall obtain a truer insight into the mimetic relationships of these insects if we take their natural behaviour as our guide, than if we rely too exclusively upon theoretical deductions based on colour patterns alone.

To take an example. We know nothing whatever about the edibility, or otherwise, of the numerous species of South American *Erycinidæ*. There appear to be a good many cases of mimicry among them, and a certain number of the species are very brightly coloured. It has therefore been supposed that the family is probably unpalatable as a whole. On the other hand, Wallace tells us (*Trans. Ent. Soc.* (2), II, 1863, p. 262) that the brightly-coloured species of *Erycina* have a very quick, jerky, "skipper"-like flight; whereas of the other genera "the great mass of the species" have the curious habit of always settling on the under-sides of leaves with wings outspread.* Now habits such as these are not known to occur among any distasteful butterflies in any part of the world; for, as we have seen, leisurely movements and a contempt for concealment are the most essential characteristics of these insects, for which the display of their warning colours is of the very first importance. In the light of our present knowledge therefore it seems difficult to justify such a far-reaching assumption of distastefulness; and we can scarce hope for stability in the theoretical edifices which may be raised on so dubious a foundation.

Again, it has been suggested that the roughly *Acræa*-like facies of the giant *Papilio antimachus* of West Africa has probably a Müllerian significance, apparently without any regard to its habits. My friend, Professor Yngve Sjöstedt, of Stockholm, who collected for some time in the Cameroons, has given me a graphic account of the great wariness and tremendous speed of this strange insect, whose flight, he said, could only be compared to that of a swallow. On the other hand, he told me that the lovely blue *Papilio zalmoxis*, which is often associated with *antimachus* by systematists, was far more common, having a slow heavy flight and being easily captured. In this case the habits serve to confirm the idea of distastefulness suggested by the appearance of the insect. But are we then to

* Bates also gives some interesting notes on the remarkable differences of habits which are to be found in this family (*op. cit.* (2), V, 1858, pp. 4, 5).

put *antimachus* in the same category, and utterly ignore that remarkable divergence in behaviour which of itself bears eloquent testimony to a profound difference between these two species in relation to their insectivorous foes?

The Pierine genus *Belenois* has also been credited with unpleasant qualities, and these are supposed to be so marked that, as recently suggested, *B. severina* has been mimicked by several species of other genera. There is nothing in the flight of this species to lend colour to such a view, and it has apparently been overlooked that in my experiments (Trans. Ent. Soc. 1902, *passim*) this insect and the closely allied *B. mesentina* were eaten by baboons with evident relish. They were also eaten without any signs of distaste by a mongoose, a kestrel and mantises; while Colonel Yerbury observed *B. mesentina* to be eaten in large numbers by spiders, and its larvæ were eagerly devoured by my baboon. The assumption of a pronounced degree of distastefulness in this case does not seem to be warranted, unless supported by experiments which shall refute the results obtained by myself.

The suggestion of inedibility in the genus *Precis* is still more instructive, and may therefore be treated more in detail.

*The suggested distastefulness of the Nymphaline genus
Precis.*

In Trans. Ent. Soc. 1902 (pp. 424-430) Professor Poulton very strongly urged the probable unpalatability of the genus *Precis*, basing his views upon the apparent conspicuousness of the under-side colouring in the wet phases of three species. For he says: "It has here been shown that there are important [warning] elements in the under-side coloration of the wet phases of *Precis sesamus* and *P. antilope* which cannot be explained as mimicry, Batesian or Müllerian, while the entire appearance of the under surface of *P. archesia* f. *pelasgis* can only be interpreted as a warning character" (*l.c.* p. 438). This conception is further supplemented by the "inevitable conclusion" that the conspicuousness of the wet phase has been modified out of the older cryptic appearance of the dry (*l.c.* pp. 430, 431); and the tentative suggestion that the former phase may be more unpalatable than the latter (p. 441).

With regard to the black, white-spotted area at the base of the under-side of the hind-wing in the wet phase of *sesamus* and *antelope*, Professor Poulton has himself recognised that this marking is not so isolated as he at first thought (p. 427). Indeed, it actually occurs in those very *Acræas* to which these insects present a rough mimetic resemblance, and therefore its appearance in *Precis can* quite consistently be explained on Batesian lines. Thus an important plank in his argument collapses.

Next as to the case of *pelasgis*, Professor Poulton says that "the conspicuous appearance of the under-sides of these forms is doubtless chiefly adapted to render them conspicuous during the attitude of rest" (p. 438). Now unlike *Danaines* and *Acræas*, I have found it no easy matter to discover a wet-phase *Precis* in an attitude of prolonged rest, and in every such case that I can recollect the butterfly had concealed itself on the under-surface of a leaf; a position which can hardly be considered to lend itself to a display of warning colours.

During my last summer in Rhodesia I kept a special look-out for *pelasgis*, and on three occasions I observed a specimen going to roost under the broad leaves of its food-plant. I trust some other entomologist will check my observations, for I must confess that I utterly failed to detect in the appearance of these insects anything which could be described, even by the widest stretch of imagination, as "startlingly conspicuous" (p. 429). On the contrary, the general effect of the colouring harmonised with the surroundings in a way one would not expect when merely examining the insect in the cabinet; for the pale transverse stripe (the so-called "warning" band) did not throw the insect into relief, but served only to break up its contour, which thus became less obvious in the lights and shadows among the leaves. I do not wish to maintain, however, that the colour of *pelasgis* is ideally procryptic; far from it. But of this I feel assured, that it would afford adequate protection to an edible species at a time when the struggle for existence is not too keen, and when the shrubs and bushes still retain sufficient leaves beneath which it may safely shelter. Nor can I think that its colouring would prove a danger to so alert and active an insect during its waking hours.

The next point to be considered is the supposition that

the brighter under-side colours of the wet phases of these species has been more recently evolved from the older cryptic pattern of the dry phase. On general grounds such a conclusion seems very difficult to accept. There can be no question that for butterflies which are on the wing throughout the year in South Africa the dry season is the time of greatest stress and danger. And from this it can only be concluded that that phase which alone is able to subsist under such conditions must present a higher degree of protective efficiency, either in colour or habits, than does the wet phase. If then it be supposed that this cryptic coloration, or some modification of it, was originally common to both seasons, it is difficult to understand why it should subsequently have been eliminated for the purpose of establishing a scheme of colouring having a lower protective value. For if this cryptic under-side afforded an efficient protection from the greater risks of the dry season, it must have been amply sufficient to meet the requirements of the species during the less dangerous summer months. A comparison of various details of the patterns also seems to me to point strongly to the opposite conclusion, namely, that the dry phase is a more recent development of the wet in response to a greater need for protection; while in the case of *sesamus*, there is important experimental evidence in the same sense. In these experiments, which are as yet unpublished, I found that by the application of moisture I could convert the dry phase into the wet; but I could not convert the wet into the dry, either by dryness or cold. If we accept Weissman's arguments in respect to *Araschnia levana*, this evidence must be taken as indicating that the wet form is phylogenetically older than the dry. Thus the suggestion that the wet phase represents an unpalatable and warningly-coloured form, which has been evolved from the cryptic dry phase, finds no support. On the contrary, the evidence points to the conclusion that the cryptic dry phase is a later development in response to a greater need for protection, and also shows that there is no adequate reason why we should postulate distastefulness in the wet phase of this genus.

Finally, we may turn to the evidence yielded by the various experiments which are detailed in the earlier pages of the same paper. In the course of these experiments examples of five species of *Precis* (including

Junonia) were offered to mantises, a spider, a kestrel, a ground-hornbill, a mongoose, a monkey (*Cercopithecus pygerythrus*) and baboons; and subsequently (unpublished) to another species of monkey, *Cerc. albigularis*. In no case did the behaviour of these animals give any grounds for the supposition that the butterflies possessed any unpleasant flavour whatsoever; and the value of the evidence is obviously enhanced by the fact that the *Precis* were readily eaten by a number of very different animals. But leaving out of consideration those animals which exhibited rather indiscriminate tastes, we may briefly summarise the remaining cases:—

- Precis antilope* (dry phase): 2 examples eaten readily by *Cerc. pygerythrus*.
P. archesia (wet): 4 eaten with relish by kestrel; also eaten by wild rock lizards.
P. archesia (dry): 1 eaten by baboon.
P. sesamus (wet): 4 eaten with relish by kestrel; 1 eaten readily by *Cerc. pygerythrus*; 5 eaten by baboons; also eaten by wild rock lizards.
P. sesamus (dry): 2 eaten readily by baboons; 12 eaten on five different occasions by *Cerc. albigularis*, which received the first with some caution, while every subsequent insect was taken with evident appreciation, the monkey cramming them into its mouth wings and all. The same animal refused *Acræa natalica* and two species of *Amauris* with evident signs of disgust.
P. ccbrene: 5 eaten with relish by kestrel; 1 eaten readily by *Cerc. pygerythrus*; 1 eaten by wild kingfisher.

The first *P. sesamus* (wet) which was given to a baboon was merely pulled to pieces without being tasted, but the remains were promptly eaten by its companion, and immediately afterwards each baboon ate another specimen. In the light of a subsequent experiment (*l. c.* p. 382), there can be little doubt that this first rejection was due to the misapprehension that the insect was an *Acræa*, to which it presents a general resemblance.

In view of all the foregoing considerations I find it impossible to entertain the idea that the genus *Precis* possesses any appreciable distasteful qualities.

The value of experiment as evidence of palatability.

The divergence of opinion which exists on the subject of palatability between the more extreme and more moderate supporters of Müller's theory practically resolves itself into a question of the relative value and reliability of the various lines of evidence available. The following are the principal sources from which information may be derived, given in the order of their importance.

- (1) Exact observation as to the insects actually eaten and avoided by wild insectivorous animals.
- (2) Careful experiments upon wild or captive animals.
- (3) Field observations on the flight and general habits of insects in relation to their environment.
- (4) The comparative study of colour patterns and structure.

The first class of evidence, which is obviously most essential, is unfortunately the most difficult to procure, more especially in the case of butterflies; for very many birds cut off the wings of these insects before eating them, and they cannot therefore be identified by an examination of the stomach contents, as in the case of insects having easily recognisable chitinous structures. Thus we must rely to a very great extent upon the three remaining sources of information.

Now in almost all those cases where the existence of unpalatability is in dispute it will be found that the arguments in its favour are based exclusively upon the fourth line of evidence. But I believe that most entomologists will agree that deductions of this kind are peculiarly liable to error unless they be supported by evidence from some other line of investigation. For my part, where I find that conclusions derived from (2) and (3) point in one direction, and those derived from (4) in another, I have little hesitation in accepting the former and rejecting the latter.

As against this, it will be contended that habits cannot be taken as an absolute proof of edibility or otherwise. For although all the butterflies that have nauseous qualities announce their presence by a characteristic demeanour, yet we must not suppose that these qualities have suddenly appeared as we now see them; on the

contrary, they will have been gradually evolved. We may therefore expect to find at the present day species in a transitional state, which, while possessing a certain degree of distastefulness, still find it necessary to retain the habits, or even the colouring, of edible forms. With this proposition I entirely agree; for it seems very probable that such cases will occasionally be found. But I fail to see that such an admission will justify a wholesale assumption of moderate distastefulness throughout all the *Pierinæ*, for example; and this is especially unwarranted in those particular cases where experimental evidence points in an opposite direction.

Here another objection is likely to be raised against me, for it will be argued that experimental evidence may at times be very misleading. Again I am quite ready to admit that there is much truth in this as a general observation. Professor Poulton insisted very strongly upon this view when commenting upon my experiments (Trans. Ent. Soc. 1902). With reference to the eating of *Acræinæ* by a ground hornbill, he says: "It has already been pointed out that the acceptance of insects by insectivorous animals in captivity is no proof of their normal likes or dislikes in a wild state. Such acceptance only proves what their action would be when they had been, from some exceptional cause, kept without their normal food in its usual quantity and variety" (*l. c.* p. 348). Unfortunately the general criticism does not happen to apply to the particular case. The bird was entirely unconfined, and wandered at will searching for his food just like his wild relatives on the next hill-side, with only this exception: if insects, etc., were scarce, the wild birds would have to go hungry or eat what they did not like, while Colonel Bowker's bird always got additional food at the house. The conditions of the experiment therefore render it highly improbable that the hornbill was eating insects which it would normally reject, and its whole demeanour was quite at variance with such a supposition.

Again, in reference to my experiments with baboons the following criticism was made: "Considering what has been already argued about insect-eating animals in confinement, the acceptances (excluding the *Hesperidæ*) probably do not justify the conclusion that the Lepidoptera were palatable, or that they would be sought for in the wild state except under the stress of hunger" (*l. c.* p. 389).

I very much regret that here likewise I am quite unable to agree to this sweeping rejection of the whole of the evidence that tells in favour of palatability, merely on an *à priori* assumption. In the carrying out of these experiments the importance of maintaining a natural diet was fully recognised, and although there will be no doubt a certain percentage of error, yet I am well satisfied that the results may be taken as giving a very fair idea as to the general likes and dislikes of these animals in regard to both butterflies and Coleoptera. Surely it must be something more than a mere coincidence that in every case where the flight or habits of a butterfly indicated the probable existence of an unpleasant taste, the baboons arrived at a similar conclusion from actual experiment. Moreover it is not quite clear why acceptance should be admitted as evidence of edibility in Coleoptera, but not in Lepidoptera.

Later on in the same paper the question of experimental evidence is summarised in the following terms: "It has already been pointed out that the refusal or evident dislike of insect food by captive animals is trustworthy evidence of unpalatability, while acceptance is not proof of palatability" (*l. c.* p. 436). This statement seems open to serious objection on two grounds. In the first place, there is too emphatic an insistence upon the possibility of error where an insect is accepted; for it practically casts suspicion upon every such case. On the other hand, the possibility of error in the other direction is not indicated. I agree that where an insect is tasted and rejected with signs of dislike, such is good evidence of distastefulness. But where an insect is merely disregarded or refused without tasting, this is not of itself reliable evidence; it may, or may not, indicate the existence of nauseous qualities. Everything depends upon the conditions of the experiment. To take a few examples. The refusal by one of my baboons of the first specimen of *Præcis sesamus* (wet) cannot be interpreted as a sign of unpalatability, for this is negated by their subsequent behaviour towards this species; the refusal was almost certainly due to either a mimetic misapprehension, or that general distrust of brightly coloured insects usually exhibited by these animals. Care also had to be exercised that too many distasteful things were not presented at once, otherwise they became very suspicious of everything offered to them.

The rejection of the first specimen of the scarlet-tipped *Teracolus achine* has likewise no significance, for on several occasions subsequently they ate fourteen similarly coloured specimens of this genus "with undoubted appreciation." Again on offering a larva of *Belenois mesentina* to the female baboon she was clearly afraid of it and tasted it most cautiously, yet on finding it all right she "eagerly devoured over twenty of them" (*l. c.* p. 385). Yet the male, which was far more timid and suspicious in temperament, "was much too frightened to eat them in spite of the example of the female." Had these larvæ been offered to the male only, it is probable that an entirely erroneous conclusion as to their extreme unpalatability would have been deduced from his behaviour. Cases of this kind might be easily multiplied, as, for instance, where unsuitable insects are offered, or where suitable insects are given to over-fed animals, and so forth.

The fact remains that even when reasonable care is exercised there must be many opportunities for error in estimating degrees of palatability or the reverse. Yet it seems a fair contention that, in the absence of obvious mistakes or inaccuracies, the true value of such experimental evidence can best be assessed by the man who actually carries out the experiments. He will be fully cognisant of all the conditions under which the experiments were made; he will presumably be acquainted with the special idiosyncrasies (often a very important point) of those animals upon which he experiments; finally, he alone is able to see and compare those subtle differences of manner, facial expression, etc., which constitute our only guide in estimating the psychological effect produced upon the animal. If similar experiments are repeated by a number of other observers the chances of error will be much diminished, and we shall thus obtain a solid foundation of fact upon which to build up those broad generalisations after which we are seeking.

A final point may be noticed. It has been suggested to me that perhaps we may be unable to demonstrate by experiment these incipient degrees of distastefulness which have been postulated for many genera of *Nymphalinxæ* and *Pierinxæ*. But if these unpleasant flavours are so slight that insectivorous animals in captivity are unable to appreciate them, it seems scarcely probable that they will have any real selection value, or that they will be

capable of producing the profound colour modifications which have been attributed to them. When an insect having such qualities mimics a really unpalatable species, it seems highly probable that the mimicry will have been due to the operation of Bates' factor and not that of Müller. For we must remember that birds have probably been the principal agents in producing these effects, and Professor Poulton has himself arrived at the conclusion that the discriminative tastes of birds are not as highly developed as those of mammals (Rep. Brit. Ass. 1887, p. 764). As he there says, this is what we should rather expect owing to the relative difference in their intelligence; and it is not therefore likely that a slightly unpleasant taste in a butterfly will have a mimetic importance in relation to birds, when it apparently remains undetected by so intelligent an animal as a baboon.

In conclusion, I must express the sincere regret I feel at having to insist so much upon the points in which I differ from my old friends Professor Poulton and Dr. Dixey, to whom I am so deeply indebted, not only for their continued personal kindness and encouragement, but also for the stimulating influence of their many valuable publications, with the general tenor of which I am entirely in accord. For although I have thought it necessary to point out what I consider to be definite limitations to Fritz Müller's principle, I have yet a firm belief in its reality as an objective factor which has profoundly influenced a large number of insects in the tropics. But I am likewise impressed with the equal importance of Bates' principle. I have at least the consolation of finding that my friend Mr. Roland Trimen is in close agreement with the views here advocated, and I have to offer him my grateful thanks for kindly checking the greater part of my manuscript, and for the valuable comments he has made thereon.

I can only hope that this discussion may serve to stimulate other naturalists in the tropics to undertake those experiments and observations which are so much needed for the furtherance of this fascinating line of research.